THE DIGESTION AND ASSIMILATION OF FOOD BY *GLOMERIS*

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Introduction

The changes occurring in decaying organic matter during its passage through the gut of a soil animal and the form and nature of the faecal pellets have been studied by relatively few workers. More information is required about this subject because of its relevance to the formation of humus, the activities of micro-organisms, the nutrient and energy cycles and the nutrition of soil animals. With these different aspects in mind the results of feeding experiments using a millipede, *Glomeris marginata* (VILLERS), are considered in this paper.

Methods

Each of the millepedes used in the tests outlined in Table 1 had the adult complement of body segments. Before the animals were fed with the test food they were allowed to feed on a litter which gave faecal pellets which were distinguishable from those produced on the test diet. All food

TABLE 1. Details of the feeding tests

Experimental animals	Number of animals per dish	Number of pots	Duration of test (days)	Food litter
(1) Mainly large females	13	6	10	Hazel, collected in January
(2) Large females . . .	10	10	18	Hazel, collected in March
(3) Large females . . .	10	20	18	Ash, collected in January
(4) Males	10	9	18	Ash, collected in January

materials were collected from the surface of a shallow soil overlying limestone and air dried at 15°—20° C. Sub-samples were weighed for feeding to the animals, for the determination of moisture content and for chemical analysis. Before being fed to the animals the litter was sprayed lightly with water and subjected to a reduced pressure of 10—20 mm of mercury. During the feeding tests the animals were kept in covered earthenware pots 20 cm in diameter and 6 cm in depth (1) or glass pots, 8 cm in diameter and 4 cm in depth (2) and (4) 10 cm in diameter and 9 cm in depth (3). The temperature and relative humidity in the pots were respectively 13° C ± 1° C and 100 %.

The animals were re-fed daily in experiment (1) and every two days in the other tests. In experiments (1) and (3) the droppings from all the pots were bulked prior to drying under vacuum at 15°—25° C (1) or at 35°—40° C (3); the uneaten food was treated similarly. The droppings or uneaten food collected from each pot in tests (2) and (4) were dried at 105° C, weighed and then bulked prior to chemical analysis.

Fats and waxes (the crude fat fraction) were extracted with diethyl ether in a Soxhlet. Total soluble carbohydrates in a hot water extract of the litter were determined with the anthrone reagent. Holocellulose was estimated using the method of WISE et al. (1946) and lignin was determined as the 72 % sulphuric acid insoluble fraction. The values given for lignin and holocellulose have been corrected for ash and nitrogen content. Carbon was determined by the SHAW (1959) method, ash by ignition at 550° C, calorific value by bomb calorimetry and nitrogen by the Kjeldahl method.

As a control, test pots containing litter but no animals were used and the litter treated as described above. Food consumption of the animals was estimated using the following formula:

$$\text{Food consumption} = F - R - \frac{CL \cdot F}{100}$$

where F = weight of food, R = weight of uneaten food and CL = % change in weight of the control litter. Assimilation of food was calculated by subtracting the weight of the pellets from the weight of food consumed.

Results and discussion

Tables 2 and 3 indicate that only small amounts of most food components were digested and assimilated during their passage through the gut. These

conclusions are similar to those reached by VAN DER DRIFT (1951), GERE (1956) and DUNGER (1958).

TABLE 2. Changes in the chemical composition of ash litter during its passage through the gut of *Glomeris* in test (3). Each value is the mean result on a dry weight basis of duplicate analyses of the same sample

Test material	Calorific value kcal. per g	Calorific value kcal. per g ashfree	% Carbon	% Nitrogen
Control	4.85	5.29	44.1	2.62
Food	4.80	5.25	42.8	2.66
Uneaten food . . .	4.90	5.28	43.8	2.67
Faecal pellets . . .	4.76	5.33	42.0	2.80

	% Crude fat	% Soluble-Carbohydrates	% Holo-cellulose	% Lignin	% Ash
Control	3.1	4.6	34	32	11.4
Food	3.6	4.6	30	34	12.0
Uneaten food . . .	3.3	4.4	33	34	10.6
Faecal pellets . . .	1.7	4.0	27	34	14.4

Assuming that the carbohydrates and fats which were consumed in test (3) contained respectively 4.0 and 9.0 kcal per g then approximately 70 % of the energy assimilated by *Glomeris* was derived from the holocellulose, 19.0 % from the crude fat and 10.5 % from soluble carbohydrates. All the assimilation figures must be interpreted with caution because of the experimental errors involved. In particular the crude fat value of 43 % is suspect because the % crude fat itself is low (Table 2); in spite of this it seems that fatty or waxy matter is partially digested. To my knowledge a lipase has not been found in the millipede gut.

The female and male *Glomeris* converted 0.29 % and 0.45 % respectively of the consumed ash litter into body tissue. Both of these conversion values are within the range of 0—4.99 % found by GERE (1956) for *Glomeris hexasticha* BRANDT. According to VERHOEFF (1928) very few *Glomeris* live to an age of 6—7 years. Most of the specimens of *Glomeris marginata* which I have found in the field have been less than 60 mg dry weight and

TABLE 3. (a) Amount of food or food component consumed per individual per day by *Glomeris*. mg or cal (Energy).

(b) % assimilation of consumed food. 95 % confidence limits are given for two dry matter values. Only estimated values based on the dry matter and energy figures can be given for carbon in (2)

Experiment		Dry matter	Crude fats	Soluble carbohydrates	Holocellulose	Lignin	Ash	Energy	Carbon	Nitrogen
(2) Hazel litter, large females (160 mg)	(a)	3.75	—	—	—	—	—	20.9	(1.7—1.9)	0.07
	(b)	7.5 ± 1.6	—	—	—	—	—	22.2	(11—19)	6.9
(3) Ash litter large females (160 mg)	(a)	11.77	0.32	0.59	3.97	3.27	1.54	55.9	5.27	0.30
	(b)	10.5	43.2	28.7	28.4	—9.4	1.5	10.2	16.0	0.4
(4) Ash litter males (51+mg)	(a)	2.78	—	—	—	—	—	14.3	1.33	0.07
	(b)	6.0 ± 1.9	—	—	—	—	—	13.3	15.3	0.3

none have been greater than 75 mg. Taking 5.0 % as a maximum value for the amount of the consumed material which is used in body-building and assuming that *Glomeris* lives for 6 years before reaching a weight of 60 mg dry weight then 1.2 g of dry organic matter must have been consumed by the animal in this period. This is equivalent to 20 g of organic matter per 100 animals per year or approximately 1.7—10 % of the annual litter fall of 200—1200 g per m^2 in deciduous woodland (VAN DER DRIFT and WITKAMP, 1959). As these values are calculated using a conservative population estimate of 100 *Glomeris* per m^2 and a high conversion value of 5 % the actual litter consumption may be much greater.

Female *Glomeris* are on the average larger than males and in my experiments they consumed larger quantities of ash litter (Table 3). As they increased in weight at the same rate as the males the females probably play a more important part in the circulation of nutrients and energy.

TABLE 4. Changes in some of the nitrogenous components of hazel litter in the gut of *Glomeris* (Test 1). I carried out this test in collaboration with Dr. O. GILBERT

Test material	Water-Soluble Nitrogenous Material			
	Amino Nitrogen (μg/g)	Ammonia Nitrogen (μg/g)	As % of Total Nitrogen	Total Nitrogen (μg/g)
Food	193	175	2.7	13,600
Uneaten food . . .	86	335	3.2	13,100
Faecal pellets . . .	103	1385	9.5	15,700

Only small amounts of nitrogen in the food were assimilated (Table 3) but the results of test (1) indicate that part of this nitrogen reappears in the droppings as free ammonia which is available to micro-organisms (Table 4). The higher pH of the droppings of *Glomeris* compared with the pH of its food (VAN DER DRIFT and WITKAMP, 1959) may have been associated with a higher ammonia content in the droppings. The increase in soluble nitrogen compounds may be a result of the death and autolysis of micro-organisms during digestion in the gut or during drying of the pellets. If the latter is the case then more micro-organisms must have been present in the pellets than in the food prior to drying. VAN DER DRIFT and WITKAMP (1959) found a larger microbial population in the droppings of

Enoicyla than in the food litter. It is possible that the soluble nitrogen compounds in the pellets represent animal excretory products but as far as is known the excretory products of millipedes have not been determined. Contrary to our results, DUNGER (1958) found only small differences between the ammonia content of the food and droppings of several diplopods and isopods.

Some ammonia is certainly present in the freshly produced droppings of *Glomeris* and other soil arthropods and LAATSCH (1948) has suggested that this forms a humus-like complex with the lignin which is also present. DUNGER (1960) concluded that there was little change in the amount of humic plus fulvic acids in organic material during its passage through the gut of a soil arthropod but the ratio of humic to fulvic acid changed slightly. In my third *Glomeris* experiment there was an increase in the amount of lignin in the litter during its passage through the gut. This apparent increase also occurs if the crude lignin percentages are uncorrected for ash and protein content or if they are corrected only for ash content. This shows that the increase is not merely a reflection of changes in the ash or protein content of the lignin and therefore it may indicate the formation of humus.

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Summary

Feeding tests showed that a millipede *Glomeris marginata* (VILLERS) utilized 6.0—10.5 % of the dry matter, 43.2 % of the crude fat, 28.4 % of the holocellulose, 28.7 % of the soluble carbohydrates and 0.3—0.4 % of the nitrogen in ash leaf litter. There was an absolute increase in the amounts of lignin and soluble nitrogen compounds in the droppings compared with the amounts in the food. It appears likely that 1.7—10 % of the annual deciduous litter fall per m^2 may be consumed annually by 100 *Glomeris*.

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Discussion

H. U. THIELE: Statements about the litter consumption of a species can be only rough estimates, because the estimates both of food consumption and number of specimens are very approximate. The conversion rate of 5 % seems too high according to Mr. Bocock's own account and a value of 0.5 % would be nearer to Mr. Bocock's data and those of GERE (1956), and also to my own investigations with *G. marginata* (THIELE, 1959). According to these figures the estimated amount of litter consumed must be considerably higher.

On the other hand an estimate of 100 *Glomeris*/m² seems too high. My investigations in different types of forests in Germany showed for *G. marginata* mean values of about 2.5—7.5 specimens per m² (THIELE, 1956). The maximum value was 24/m². Besides there are other species of *Glomeris*, which are much less numerous. It may be that some small specimens have been overlooked, but these animals are of little importance for litter decomposition. DUNGER (1958) found in 2 cases about 30 *Glomeris*/m², but these figures depend on calculations from only one specimen caught in each sample.

In spite of these differences I came to a similar estimate of litter consumption by *Glomeris*, namely about 5 % of the total annual litter fall, but I think we need further investigations to establish the reliability of such a value.

A. BURGES: May I make a plea for more careful use of the word lignin in proximate analyses. In most work this represents only material insoluble in 72 % sulfuric-acid. In fresh plant material this is usually a good approximation to lignin, but where decomposition has occurred it may have very little relation to the true lignin content.